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THE DISTRIBUTION OF THE CHAETOGNATHA OF THE SOUTHERN OCEAN

by

P. M. David

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P. M. DAVID

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THE DISTRIBUTION OF THE CHAETOGNATHA OF THE SOUTHERN OCEAN

By P. M. David

(Plate X; Figs. 1–13)

INTRODUCTION

A NUMBER of reports on antarctic Chaetognatha have been already published (Steinhaus, 1900; Fowler, 1907; Ritter-Zahony, 1909, 1911; Germain, 1913; Jameson, 1914; Johnston and Taylor, 1921; Burfield, 1930; Bollmann, 1934; Thiel, 1938; Ghirardelli, 1953), but in most cases the collections reported on were small and restricted both in horizontal and in seasonal range.

The Discovery collections cover nearly all areas of the Southern Ocean in all seasons of the year, and from this material it is possible not only to compile a complete list of species present, but also to discover quite a lot about their distribution and something of their life histories. The approach to the subject adopted here is essentially distributional rather than systematic.

While working on *Sagitta gazellae* I also assembled data on the other species in the collections, and was struck by the very consistent pattern of vertical distribution of the commoner chaetognath species. This pattern was not clearly demonstrated in the earlier reports on antarctic chaetognaths, and it seemed worth while to attempt to show it in the present paper.

Throughout this paper the name 'Southern Ocean' has been employed to describe all that ocean which lies between the subtropical convergence and the Antarctic continent. This area is divided into two zones, the subantarctic and the antarctic, which are separated by the antarctic convergence. While it has been held by some authorities that the Southern Ocean is not a geographical entity, there is no doubt that it has at least a faunistic unity and is therefore a term of considerable value to those working on the distribution of animals in the southern hemisphere.

ACKNOWLEDGEMENTS

I am greatly indebted to Mr J. W. S. Marr for advice and for the loan of his notes on chaetognaths from the second and fourth commissions of Discovery II (1931–3 and 1935–7). These have enabled me to check many points arising from the work and have considerably lightened the task of searching through the collections for stray exotic species. I am also grateful to Mr A. Styles for preparing the diagrams for publication.

MATERIAL AND METHODS

All the material used for this study has been taken from the collections made by ships of the Discovery Committee and subsequently of the National Institute of Oceanography. It would, of course, be best if all the chaetognaths in the collections could be used for this work, but the immense labour involved in sorting and identifying them from the large number of samples available would not be repaid by the results, and therefore an attempt has been made to manage on a limited number of stations chosen from many radiating lines and many other scattered stations. For a start it was desirable to find a line of stations which extended from the subtropics southwards to as near the Antarctic continent as the ice conditions would permit. The line chosen was that worked in March 1937 on the Greenwich meridian (0°) (see Fig. 1). This gives a close approximation to typical summer conditions. In order to

verify that the pattern of distribution found in that line was not peculiar to one area, a line in 80° W (in the Pacific Ocean sector) and another in 90° E (in the Indian Ocean sector) were also examined. The line in 80° W was also worked in March, and that in 90° E in February, so seasonal differences should not affect the comparison greatly. In addition to these summer lines it was obviously desirable to find out if the pattern of distribution altered much in winter, and for this purpose a line of stations in 0° worked in August 1938 was chosen, and by analogy with the consistent pattern of distribution shown by the three summer lines it was considered that the winter pattern of distribution in 0° could be taken as circumpolar. There were two lines of stations worked in August in the Indian Ocean sector

Fig. 1. The positions of the stations used for the sections (Figs. 3, 5, 7, 8, 10, 11 and 13), the positions of the convergences and the approximate northern boundaries of the Weddell and East Wind Drifts. STC = Subtropical Convergence. AC = Antarctic Convergence. WD = Weddell Drift. EWD = East Wind Drift. O = Summer Stations. X = Winter Stations.

(though none in the Pacific in that month) which could have been used for comparison, but owing to the bad weather so prevalent in the Antarctic at that time of year neither of them was complete, and a precise comparison would have been unsatisfactory. Inspection of the samples, however, shows that the winter distribution of the Chaetognatha there is quite in line with what is found in 0°.

The data used are those from the 70 cm. vertical closing nets (N 70 V) fished through horizons from 1500 m. to the surface (the horizons being 1500–1000, 1000–750, 750–500, 500–250, 250–100, 100–50 and 50–0 m.). While these nets do not sample adequately the larger zooplankton, there is no doubt that the medium- and small-sized animals are taken satisfactorily, and the advantages of having nets which have fished accurately known depths, which have been closed before being

brought to the surface, and which do not catch anything while being lowered, far outweigh the slightly erratic manner in which the larger animals are caught. In so far as the Chaetognatha are concerned it is only the large specimens of *Sagitta gazellae* and *S. maxima* which are to some extent missed by the nets, the other species being small enough to be adequately sampled.

The results, corrected to represent numbers per 250 m. haul (Mackintosh, 1937, p. 377), have been plotted by contours of density of numbers in the manner of a physical section for temperature, salinity, etc. This method of plotting has many limitations; the stations may be widely spaced and one may question the legitimacy of presuming that any population of animals is continuous over the hundred miles or so between stations. When there are small numbers of animals, this objection is probably valid; yet the consistency of the pattern of distribution shown by the sections (Figs. 3–8) is surely evidence that the method of presenting the data is not badly at fault; for if the populations consisted of randomly spread, small patches of animals, it is unlikely that such patches would be found at two or three stations in such similar numbers that they could be plotted by the contour method with the results shown, and further, even if the populations were patchy but not randomly spread, as is quite likely, then the contour section will show the area of abundance of such patches, which is, after all, what is required. One disadvantage of the use of nets, such as the N 70 V, which fish through relatively wide horizons, is brought into prominence by the use of the contour-plotting method; that is, that a haul containing a large number of two or more species has to be plotted as if both species occupied the same place in the water column, yet it is quite likely that on occasions when the net has passed through two (or more) water masses in one haul the plankton populations are as separate as the water masses themselves.

No subsampling has been done except possibly in the 80° W line where the numbers given by Mackintosh (1937) have been used. In this line, however, the northernmost stations have been re-examined for subtropical species which might have been missed in the original sorting which was done in conditions unfavourable for the careful microscopical examination required to identify, for example, very young specimens of *Sagitta serratodentata*. The fact that some of these have now been found does not in any way affect the conclusions reached in that paper.

In addition to these lines of vertical nets, consideration of other vertical and oblique net data has been necessary to describe the distribution of the rare and the exotic species which are sometimes found in the Southern Ocean but which did not happen to occur in the four lines of stations used to describe the distribution of the commoner species.

A SUMMARY OF THE SPECIES OF CHAETOGNATHA FOUND IN THE SOUTHERN OCEAN

The chaetognath fauna can be conveniently considered as composed of three elements: (i) 'endemic' species, (ii) species common to other regions which maintain themselves in the Southern Ocean, and (iii) exotic species which probably do not maintain themselves in the area but which are carried in presumably by water movements from other regions. In addition there are a few species reported by various authors as occurring in the area, but which have not been found in the extensive Discovery collections and which are probably the result of misidentification or mistakes in labelling.

I. 'Endemic' species

(*a*) *Sagitta gazellae*

Sagitta gazellae Ritter-Zahony, 1909. *Die Chätognathen der Gazelle-expedition.* Zool. Anz. xxxiv, pp. 787–93.
S. gazellae Ritter-Zahony, 1911: Germain, 1913; Jameson, 1914; Burfield, 1930; Bollmann, 1934; David, 1955.
S. hexaptera Steinhaus, 1900; Fowler, 1907; Germain, 1913.

Sagitta innom. Fowler, 1908.
S. lyra Johnston & Taylor, 1921; Bollmann, 1934 (part); Thomson, 1947 (part).
S. maxima group Thiel, 1938 (part).

I have discussed the validity of this species in a previous report (David, 1955) and have shown that it is separate from *S. lyra* with which it has been frequently considered synonymous. In the Southern Ocean it exists in two main forms or races. One is predominantly subantarctic and the other is predominantly antarctic. These two forms can be distinguished at all stages, except perhaps at the very youngest ones. It is possible that they should be regarded as subspecifically, or even specifically distinct.

HORIZONTAL DISTRIBUTION. Circumpolar, limited in the north by the subtropical convergence, and in the south by the antarctic continental slope. Its maximum abundance is in the subantarctic.

It should be noted here that very large specimens (up to 64 mm.) of *S. lyra* have been reported by Tchindonova (1955) from the Kurile-Kamchatka trench, and from her Table 1 (p. 300) it looks as if these specimens closely resemble *S. gazellae*, especially in the tail-segment percentages (10–15·4). However, on p. 299 she records that many of these specimens had fully developed ovaries 'reaching as far as the ventral ganglion, in some cases indeed nearly to the region of the head'; it is therefore apparent that these specimens cannot be *S. gazellae*, for, at maturity stage III[1] and beyond, all the posterior teeth are lost in that species (David, 1955, pp. 243, 259), whereas the smallest number of posterior teeth in the Kurile-Kamchatka specimens is 6 (at 47 mm.). It seems unlikely that these specimens are *S. lyra* either, for the smallest number of hooks is 4–5 (at 64 mm.) and is more usually 6 or 7, whereas at maturity stages III and IV *S. lyra* has 3 or even less (Tokioka, 1939; Hamon, 1952; David, 1955). It seems probable that these specimens are *S. maxima*, despite the very small tail percentage given, for the head armature numbers fit that species well, as does the size range and the fact that *S. maxima* is found in a similar environment in the North Atlantic. Examination of the paths taken by the nerve cords from the ventral ganglion would have settled the question had the specimens been figured, for in *S. maxima* the two posterior cords run down the inner margins of the fins on the ventral side giving off branches to the fins at intervals, whereas in *S. lyra* and *S. gazellae* these cords run direct to the anterior insertion of the fins where they divide to run down the inner margins of the fins on both the ventral and dorsal sides.

(*b*) *Sagitta marri*

Sagitta marri David, 1956. *Sagitta planctonis and related forms*. Bull. Brit. Mus. (Nat. Hist.), Zool. IV, 8, pp. 435–51.
S. zetesios Fowler, 1907.
S. planctonis (non Steinhaus) Ritter-Zahony, 1911 (part); Jameson, 1914; Johnston & Taylor, 1921; Burfield, 1930 (part); Bollmann, 1934 (part); Mackintosh, 1937; Thiel, 1938 (part).
S. planktonis (non Steinhaus) Hardy and Gunther, 1936.

Ritter-Zahony recognized that this antarctic form differed from its close relations in warmer oceans, but, for reasons which I have discussed elsewhere (David, 1956), regarded it as an intermediate form between *S. zetesios* Fowler and *S. planctonis* Steinhaus. It is shown to be a separate species by the shape and position of the seminal vesicles, and by other anatomical features.

HORIZONTAL DISTRIBUTION. Circumpolar; its maximum abundance is in the Antarctic.

[1] Following Kramp (1939) I distinguish five stages of maturity numbered I–V for the common antarctic chaetognaths, stage I being the immature forms and stage V the spent animals. At stage III the seminal vesicles are full and the ovaries somewhat enlarged. At stage IV the ovaries are fully developed and breeding takes place. From most points of view the distinction between stages III and IV is slight, and animals in both stages may be regarded as fully mature.

(*c*) *Eukrohnia* sp.

E. fowleri Ritter-Zahony, 1911 (part).

This form, which was considered to be *E. fowleri* by Ritter-Zahony, appears on careful examination to be a species in its own right. The number of teeth, the absence of eye pigment, and other points separate it from *E. fowleri*. It will be described and named in a separate publication.

Horizontal distribution. Circumpolar, northern limits not known, but it has not been found in the Discovery collections north of the subtropical convergence. It is possible that it may be found in other oceans, but it seems at present to be an endemic form.

II. Species common to other regions

(*a*) *Sagitta maxima*

Sagitta maxima (Conant) 1896.
Spadella maxima Conant, 1896, Johns Hopkins Univ. Circ. 15, p. 84.
Sagitta whartoni Fowler, 1896.
S. gigantea Broch, 1906.
S. maxima Ritter-Zahony, 1911; Germain, 1913; Jameson, 1914; Huntsman, 1919; Burfield, 1930; Bollmann, 1934; Thiel, 1938 (part); Fraser, 1952.
S. lyra Michael, 1911 (part).

Doubts have been expressed about the validity of this species, notably by Michael (1911, 1919) and Thomson (1947), but it is in fact an easily recognizable form which can be differentiated from its near relatives *S. lyra* and *S. gazellae* by its greater tail-segment percentage, the position of the commencement of the anterior fins, and the position of the seminal vesicles.

The Southern Ocean form of this species is considerably smaller than its arctic counterpart (see Plate X). The latter has been reported at more than 90 mm. in length (Fraser, 1952), whereas 55 mm. appears to be the maximum length of the southern form. It can be seen from Plate X that the arctic specimen is, apart from its much greater length, a far more massive creature than the southern specimen. It seems quite possible that a careful study of these two forms would reveal, at the least, sub-specific differences between them.

Horizontal distribution. Circumpolar in the West Wind Drift, most abundant in the subantarctic zone. It is apparently absent from the more tropical parts of the Indian Ocean, as it was not found in the two series of stations in 90° E made between 30° S and the equator, where nets were fished to 1500 m. (stations 2683–91 and 2886–96). It occurs in the Benguela Current as far north as 22° 48′S, Station W.S. 976 (Station List 'William Scoresby' 1950, 1953), and Thiel may have found it further north in the Atlantic, though his records may well have been of *S. lyra* which he failed to distinguish from *S. maxima*. In the Peru Current it occurs as far north as 04° 20·4′ S, Stations W.S. 701 and 722, though three of the specimens taken in this area were far from typical of either the arctic or antarctic forms, resembling *S. lyra* in many features. Table 1 shows a comparison of the Peru Current specimens with two subarctic specimens and a series from the Southern Ocean. Whereas the arctic and Southern Ocean forms have very similar armature formulae at the same stage of maturity (though at very different lengths), the Peru Current specimens show a very considerable reduction of head armature with advancing maturity. It seems possible that a study of the Peru Current population of *S. maxima* might shed considerable light on the phylogenetic relationships of the group of chaetognaths composed of *S. lyra*, *S. gazellae*, and *S. maxima*.

(*b*) *Sagitta macrocephala*

Sagitta macrocephala Fowler, 1905, *The Biscayan Plankton of H.M.S. Research*. Trans. Linn. Soc. London, Ser. 2, vol. x, p. 65.

S. macrocephala Fowler, 1906; Ritter-Zahony, 1911, 1914; Germain & Joubin, 1916; Michael, 1919; Bollmann, 1934; Thiel, 1938; Tokioka, 1939; Fraser, 1952.

An easily recognized species. The antarctic specimens appear to be identical with those from other oceans.

HORIZONTAL DISTRIBUTION. Widespread in all deep oceans, circumpolar, but always in small numbers.

Table 1. *Comparison of the length and head armature of specimens of* S. maxima *at Stages III and IV of maturity, from the Arctic, Antarctic and Peru Current*

Length	*Tail segment*	%	*Hooks*	*Anterior teeth*	*Posterior teeth*	*Ovary*	%	*Seminal vesicles*	*Station no.*	*Depth*
					Arctic					
84	17	20·3	5/5	5/5	6/6	26	31·0	pres.	3227	1000– 750
73	15	20·6	6/6	5/5	7/7	13	17·8	pres.	3227	1500–1000
					Antarctic					
55	12	21·8	5/6	4/5	6/7	12	21·8	pres.	1729	1500–1000
46·5	11	23·7	7/6	?	6/6	19/17	41·0	pres.	2584	1500–1000
46	11	24·0	5/5	4/4	7/7	16/8	34·4	pres.	2849	1000– 750
44	10	22·8	5/5	4/5	6/5	5	11·4	pres.	993	1000– 750
44	11	25·0	5/5	6/6	?	7	15·9	pres.	666	1000– 750
43	10·5	24·5	6/5	4/4	6/6	10	23·1	pres.	2451	1000– 750
					Peru Current					
38	7·5	19·7	3/3	2/2	3/3	8·5	22·5	—	WS 612	1000– 750
35	8	22·8	3/4	2/2	2/1	15·5	44·5	—	WS 701	1000– 750
35	8	22·8	3/3	2/2	3/1	5	14·3	—	WS 606	1000– 750

(*c*) *Eukrohnia hamata*

Eukrohnia hamata (Möbius), 1875.

E. hamata[1] Ritter-Zahony, 1909, 1911; Jameson, 1914; Johnston & Taylor, 1921; Burfield, 1930; Bollmann, 1934; Hardy & Gunther, 1936; Mackintosh, 1937; Thiel, 1938; Ghirardelli, 1953.

Spadella hamata Grassi, 1883; Fowler, 1896.

Krohnia foliacia Aida, 1897.

K. hamata + *K. hamata* var. *borealis* Moltschanoff, 1907.

K. hamata Hertwig, 1880; Langerhans, 1880; Conant, 1896; Krumbach, 1903; Fowler, 1905, 1906.

This well-known species exhibits a great deal of variation in size. In the Southern Ocean there are two clearly defined races more or less separated by the antarctic convergence; and the specimens from subtropical waters seem to belong to a smaller race also. *E. hamata* var. *antarctica* Johnston & Taylor is the spent form which seems able to live for a while after spawning.

HORIZONTAL DISTRIBUTION. Cosmopolitan in the deep oceans, circumpolar, maximum abundance (in the Southern Ocean) in the vicinity of the antarctic convergence.

(*d*) *Heterokrohnia mirabilis*

Heterokrohnia mirabilis Ritter-Zahony, 1911, *Revision der Chaetognathen*. Deutsche Sudpolar Exped. Bd. XIII (5), p. 42.

H. mirabilis Tchindonova, 1955.

[1] Only those authors who have examined antarctic material have been included in the synonymy under *E. hamata*.

This remarkable species was first described from eight specimens in the Gauss collections which were taken in deep hauls (3423–2000 m.) from far south in the antarctic zone. Only one further specimen has been reported, that found by the Russian expedition to the Kuriles trench which was taken between 5000 m. and the surface (Tchindonova, 1955). The specimen reported as *H. mirabilis* by Jameson (1914) seems, from its head armature, to have been a damaged specimen of *E. hamata*.

Two specimens have been found in Discovery collections (Station 661, 3000–2000 m.), but neither of them is in good enough condition to determine the precise shape of the fins, and it seems worth while considering whether these specimens could be distorted examples of some better-known form. The presence of transverse musculature on the tail segment was regarded by Ritter-Zahony as a point of great importance ('the tail has no homologue in any hitherto known chaetognaths'), but Tokioka (1952, p. 312), referring to *Zahonya cestoda* van Oye (an enigmatic deep-living chaetognath), remarks: 'It is a noteworthy fact that some species with strongly developed musculature assume an appearance when they are in a strongly contracted state, as if they were provided with a transverse musculature along the whole body.' This appearance can occasionally be observed in specimens of *E. hamata*. The Discovery specimens of *H. mirabilis* do show transverse musculature in the tail, but they do not appear to be at all strongly contracted. The number of anterior teeth in this species (see Table 2) is strikingly large in comparison with other antarctic deep-water forms (15, as compared with 10 in *S. macrocephala*, and 8 in *S. marri*), and, as Ritter-Zahony has pointed out, only *S. helenae* (a tropical epiplanktonic species) has comparable numbers. Ritter-Zahony records that the gut of the largest of his specimens was brick red when fresh, and although the colour has faded from the Discovery specimens the appearance of the gut is the same as that in specimens of *S. macrocephala* and *E. fowleri*, both of which have a red gut when fresh.

Ritter-Zahony was unable to find any eyes in his specimens, and both Discovery specimens are also apparently without eyes. Neither of the Discovery specimens has ripe seminal vesicles, but the smaller animal has rudiments of them in the same position as those figured by Ritter-Zahony in his fig. 46. From the tail-segment percentage and general appearance the most likely species which could be confused with *H. mirabilis* is *S. macrocephala*, but the vestibular organ in these two species is quite different, being quite smooth in *H. mirabilis* (see Fig. 2) and distinctly papillated in *S. macrocephala*, and although Ritter-Zahony stated that in young specimens of *H. mirabilis* small papillae were present, they are present in *S. macrocephala* at all sizes. Ritter-Zahony did not record *S. macrocephala* from the Antarctic, yet it is not an uncommon species in the Discovery collections and this would lead one to suspect that *H. mirabilis* was indeed a damaged specimen of that species. Nevertheless, bearing all these possibilities in mind I am convinced that *H. mirabilis* is a valid species, though I feel that really perfect specimens might show that it should belong to the genus *Sagitta*.

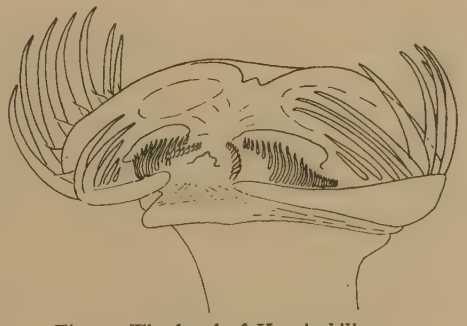


Fig. 2. The head of *H. mirabilis* seen from an antero-dorsal direction.

Horizontal distribution. Antarctic, between 64° 29′ S—65° 18′ S and 80° 00′ E—85° 27′ E (Gauss), Discovery Station 661, 57° 36′ S 29° 54′ W. North Pacific.

III. Exotic species

This group is composed of seven species which will not be discussed in detail as they are all sub-tropical or tropical forms which almost certainly do not maintain themselves in the Southern Ocean.

(*a*) *Sagitta hexaptera* (d'Orbigny)

A widespread species in subtropical and tropical seas with a considerable tolerance for the colder parts of those areas; mainly an inhabitant of the surface 100 m.

(*b*) *Sagitta lyra* (Krohn)

A widespread species in subtropical and tropical seas, having a slightly greater tolerance than *S. hexaptera* to cold water. Normally an inhabitant of the water layers below 100 m. though infrequent below 500 m.

(*c*) *Sagitta decipiens* (Fowler)

A widely distributed form typical of the water layers below 100 m. in the tropics and subtropics.

Table 2. *Length and head armature of all specimens of* H. mirabilis *so far reported*

Length	*Tail* %	*Hooks*	*Anterior teeth*	*Posterior teeth*	*Depth* (*m.*)	
19	32·7	11/11	14/15	33/?	3423	Ritter-Zahony, 1911
18·6	32·3	10/9	15/15	29/30	3000	
12	33·3	?/10	10/11	25/?	3000	
10	35	11/11	?/5	6/6	3000	
10	35	—	—	—	2000	
9·4	40	9/9	—	1/1	3000	
9	35·5	8/9	?/4	2/1	3000	
8	37·5	9/9	4/4	1/1	3000	
36	44·4	14/14	13/13	14/16	5000–0	Tchindonova, 1955
33	39·5	11/12	10/9	29/22	3000–2000	Discovery collections
10·2	36·3	8/8	3/?	1/1	3000–2000	

(*d*) *Sagitta minima* (Conant)

The distribution of this species is not at all well known, but it is common in the subtropics of the southern hemisphere.

(*e*) *Sagitta serratodentata* Krohn

A very widely distributed form which exhibits considerable, possibly specific, variation. The most cold-tolerant of the exotic species considered here, it normally inhabits the surface water.

(*f*) *Sagitta zetesios* Fowler.

An inhabitant of deep water, usually below 750 m., in tropical and subtropical waters.

(*g*) *Krohnitta subtilis* (Grassi)

This is a common subtropical species usually in the 250–100 m. layer, but it is occasionally found in surface hauls.

(*h*) *Pterosagitta draco* (Krohn)

A common surface form in warm latitudes.

None of these species is common in the Southern Ocean, but all have been found, usually as single specimens but occasionally as several together, at some time in the Discovery collections made south of the subtropical convergence. None of these species has been found in Discovery collections made south of the antarctic convergence, and usually they are not found more than two or three degrees south of the subtropical convergence. Previous authors have recorded some of them in the Antarctic

and in view of the absence of Discovery records to confirm them it seems probable that most of these anomalous records can be regarded as misidentifications of badly preserved material. For example, *S. hexaptera* has been reported from the Antarctic by Fowler (1907), Ritter-Zahony (1911), Germain (1913), and Johnston & Taylor (1921). In all these cases, except that of Ritter-Zahony, confusion with specimens of *S. gazellae* on which the fins were damaged seems to be the most likely explanation; after 1921 the same confusion does not seem to have arisen, although, surprisingly enough, very recently three large specimens of *S. hexaptera* were reported from the Mediterranean as specimens of *S. gazellae* (Furnestin, 1953, 1955). In the case of Ritter-Zahony (1911) there can be little doubt that the specimens reputedly from 66° 2′ S 89° 38′ E were *S. hexaptera*, since he was very familiar with that species and with *S. gazellae*, but it is significant that in the same haul he found *K. subtilis*, another subtropical species, and it is possible that there may have been confusion with a haul made on the same date (22nd November) in 1901 (not 1902 as reported) when the ship's noon position was 34° 9′ S 17° 26′ E in the vicinity of Cape Town where one would expect to find these two subtropical species. *S. serratodentata* has been reported by Burfield (1930) from the Ross Sea. Only one specimen was taken, and the only explanation I can suggest is contamination from a more northerly sample. It is quite easy for a specimen to be caught inside the lid of a sample jar and the lid to be put on to another jar, or for a single specimen to be left under the rim of a petri dish while sorting. Several authors have recorded the species from the northern part of the Subantarctic where its presence can be confirmed by Discovery records.

IV. Doubtful species

S. neglecta. This tropical species was reported by Johnston & Taylor (1921) from 64° 34′ S 117° 1′ E, and must be regarded as a case of mistaken identification. The species is rare even in subtropical waters and certainly does not occur in Discovery collections from the Southern Ocean.

VERTICAL DISTRIBUTION

The vertical distribution of the relative density of the populations of chaetognaths is shown in Figs. 3, 5, 7, 8, 10, 11, 12 and 13 on three lines of stations, one in the Atlantic sector (meridian of 0°), one in the Indian Ocean sector (meridian of 90° E) and one in the Pacific Ocean sector (meridian of 80° W).

Before comparing the results from these sections it is necessary to indicate that there are certain obvious physical differences involved. The line in 90° E is perhaps the most simple; it is relatively long and the subantarctic zone extends from about 40° S to about 52° S, both convergences being rather indistinct. The antarctic zone was accessible from about 52° S to the ice edge in 65° S. Only Station 2812 in this line is within the area of the East Wind Drift. The line in 0° is rather longer than that in 90° E, and it has some rather peculiar physical characteristics. The subantarctic zone extends from a fairly sharp subtropical convergence in 39° S to a rather diffuse antarctic convergence in about 50° S. The antarctic zone was accessible thence to nearly 70° S. This zone is, however, complicated by the presence of the Weddell Drift, a broad tongue of cold water originating in the Weddell Sea and deflected by the coast of Grahamland in a north and easterly direction. Deacon (1936) shows its northern limit to be in about 52° S in 0° and its southern boundary is probably in about 61° S, though it is difficult to define accurately, and both limits indeed are no doubt to be taken as tentative and subject to variation. Stations 2010 and probably 2012 lie within the influence of the East Wind Drift, and it is possible that there may be swirls or eddies between the East Wind Drift and the Weddell Current (Marr, personal communication). The line in 80° W is the shortest of the three, and the surface isotherms show that considerable north/south compression of the water masses takes place in this area. The width of the subantarctic zone is not known, since the position of the subtropical convergence has

never been determined in that part of the eastern Pacific. The presence of a few specimens of *S. serratodentata* at the northernmost station of the line (1320) suggests that the subtropical convergence might be within 200 miles or so of that position, for the species is found elsewhere in the subantarctic only within that distance of the subtropical convergence. The isotherms off the coast of southern Chile run parallel to the coast (Gunther, 1936) and this suggests that there may be a southward loop of the convergence lying from about 45° S 90° W to about 53° S 80° W and thence northward in the meridian of about 77° W (see Fig. 1), but there is no hydrological information other than that mentioned to back up this view. In 80° W the subantarctic zone extends to a fairly sharp convergence in 63° 30′ S and the antarctic zone was accessible thence to 68° 18′ S.

In view of the differing length of the three lines, the antarctic convergence has been used as a point of reference in the diagrams.

For making the sections shown in Figs 3, 5, 7, 8, 10, 11, 13 the data given in Tables 4 *a–c* (p. 225) were used. The contours adopted indicate the following quantities in terms of numbers per 250 m. haul:

	Summer	*Winter*
S. gazellae	1–5–10–20–40	1–5–10–20
S. marri	5–10–20	1–5
S. maxima	4–10–30	1–5–10
S. serratodentata	2–20–400	
S. decipiens	1–10–20	
E. hamata	1–20–100–200	1–15–50–100

It will be seen that the contours are not the same for all the species, and this is due to the very large differences in total numbers of the species present. Originally the contours were chosen by a simple progression, e.g. 5–10–20–40, but it was found that in certain species strict adherence to this method produced rather confused-looking sections, and a certain amount of allowance had to be made. In *S. maxima* and *S. marri*, for example, it was not felt necessary to indicate occasional stray specimens obviously separated from the main population, and as a result the contours for these two species begin at 4 and 5 respectively. In *S. maxima*, examination of the data showed that contours at 20 and at 40 would be an additional complication which would show nothing more than a single contour at 30. It should perhaps be pointed out that more contours tend to emphasize the separateness of the species shown in the maximum density sections in Fig. 12, but the extra amount of lines and shading tend to make the figures look confused. *S. serratodentata* has a relatively compact population and when it is present in large numbers they are really large, e.g. 620 and 715 for single hauls in 0° and 90° E, and it was not thought necessary to indicate any more than the contours given. *S. decipiens* also shows a similar compactness with smaller numbers. *E. hamata* is often present in large numbers, and it was not thought that contours between 20 and 100 would show anything better than the two at those densities.

For the winter sections where the numbers of all species were lower, lower contours were used and these have followed the simple progression except in the case of *E. hamata*, where again the intermediate contours seemed to be unnecessary.

S. gazellae (Fig. 3). The northern limit of the species is shown to be just north of the subtropical convergence in 0° at a depth of 200 m. and probably it is at a similar point in 90° E though at less depth, but in this line there is no negative station north of 2802 to prove it, though there is little doubt that the northern limit is near the convergence (David, 1955). In 80° W it is evident that the species extends well north beyond Station 1320 which is well south of the subtropical convergence. The southern limit in 0° is probably just at the continental slope, though there is not a negative station at the southern end of this line. In 90° E the species does not extend nearly so far south but ceases in

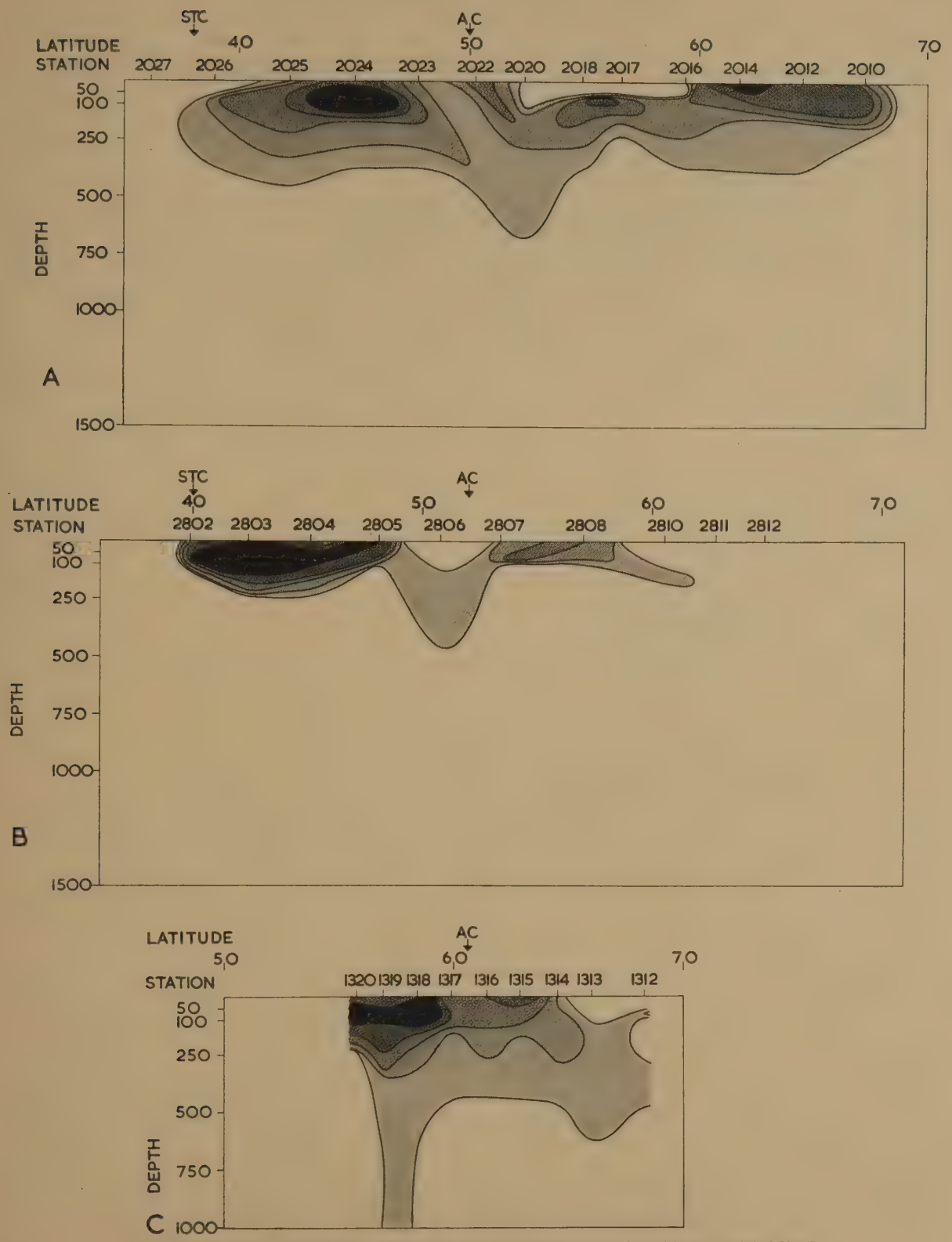


Fig. 3. The vertical distribution in summer of *S. gazellae* in 0° (A), 90° E (B) and 80° W (C).
For the numbers taken in each net see tables 4 *a–c* (p. 225).

62′ S some 180 miles short of the ice edge (Station 2812). In 80′ W the species extends, in small numbers at least, right to the ice edge (Station 1312). In all the sections for the summer months it can be seen that this species is not common below 250 m. but Table 4 shows that it does extend in small numbers to 1000 m. In each section there is an extension into deeper water in the region of the antarctic convergence, and the same phenomenon has been noticed in other sections not figured here. It may be due to the sinking of the surface waters in this region.

The main concentration of the species in each line is in the subantarctic, but in 0′ there is another concentration south of 60′ which is not paralleled in either 90′ E or 80′ W, though there is a lesser concentration in about 55′ S in 90′ E and in 63–64′ S in 80′ W, which is probably comparable with a small concentration between 100 and 50 m. in 55–56′ S in 0′ Possibly the presence of the Weddell Current in 0′ prevents this concentration from being a surface one as are those in 90′ E and 80′ W. It seems likely that the large antarctic concentration in 0′ is a feature unique to that particular area and it is tentatively suggested that its presence is in some way caused by the eddies or swirls between the East Wind and Weddell Drifts which have been already mentioned (p. 209).

Fig. 4 shows the catches of *S. gazellae* in 0° plotted against temperature and salinity and indicates how wide a tolerance the species has, though it can be seen that the largest concentrations are restricted to a narrow range of salinity. The concentrations above 20 per 250 m. haul are found between 33·94 and 34·46‰ with a temperature range of −0·18° to 11°.

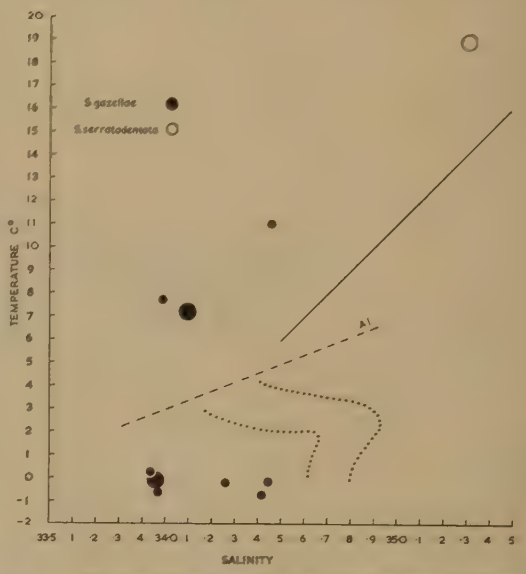


Fig. 4. The relative distribution of the two highest orders of abundance of *S. gazellae* and *S. serratodentata* in the 0° meridian in March plotted against temperature and salinity. The line A1 represents the core of the antarctic intermediate water, the two broken lines the approximate boundaries of the warm deep water, and the solid line the core of the South Atlantic central water.

Much of this information, together with further details, is given in a separate paper on *S. gazellae* (David, 1955).

S. marri (Fig. 5). The northern limit of this species is rather variable, since occasional specimens get carried north by the antarctic intermediate water, but the northern limits of the main concentrations are clearly south of the antarctic convergence. The southern limit appears to be the antarctic continental slope. From the three sections shown, the extreme northern limits are found to be 43½° S in 0°, 48° S in 90° E and 63½° S in 80° W. This wide latitudinal difference is explicable partly by variations in the latitude of the antarctic convergence, and partly by the exceptional absence of any considerable numbers of the species in the subantarctic in the 80° W line. It will be seen that the northernmost part of the main concentration in each line is 180 miles from the convergence in 80° W, 240 miles from it in 90° E, and 330 miles from it in 0°. The species is commonest between 200 and 600 m. but extends in smaller numbers to 1500 m. and occasionally more. The subantarctic specimens are never found in the surface layers, that is above 150 m., but they may extend to 1500 m. though always in small numbers. In the Antarctic the species is not at all uncommon in the surface 100 m., that is, in the antarctic surface water, but this shows only in one of the vertical sections, that in 80° W. However, Baker (1955) records *S. planctonis* (= *S. marri*) in 39% of the N 100 B nets fished in the antarctic surface layers.

The main concentrations of *S. marri* are in the warm deep water, as reference to the temperature/

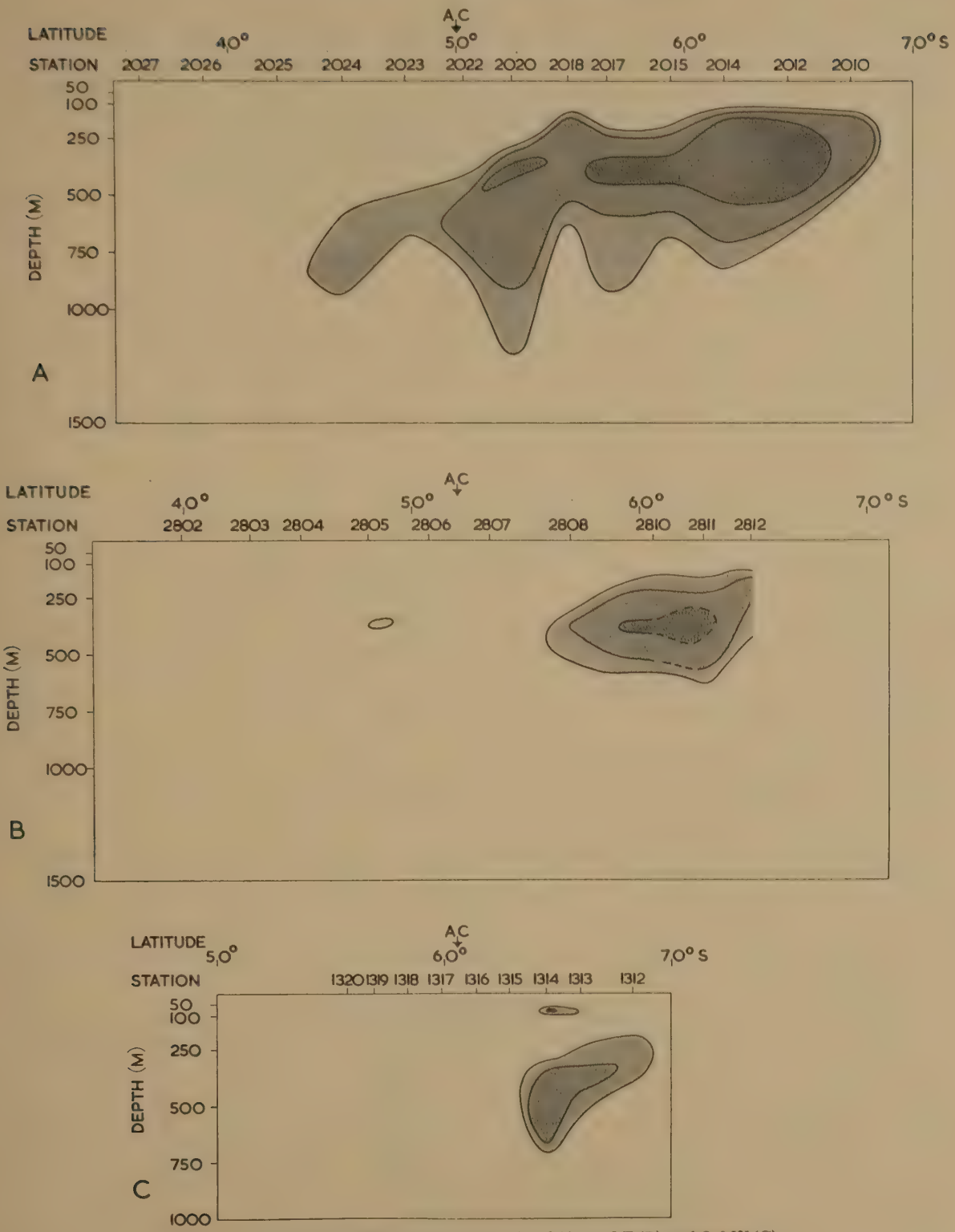


Fig. 5. The vertical distribution of *S. marri* in 0° (A), 90° E (B) and 80° W (C). For numbers taken in each net see tables 4 *a–c* (p. 225).

salinity diagram (Fig. 6) shows. The very narrow tolerance range of the maximum concentrations of the species, 34·67–34·71 ‰ and 0·1 to 1° C, suggests a restricted distribution, but within these limits is a very large mass of water, and the section in 0° (Fig. 6) shows indirectly how extensive this water mass is. The temperature/salinity diagram also shows clearly how parts of the population are 'lost' by being carried north to the antarctic intermediate water. These 'sterile expatriates' (Ekman, 1953) are probably lost mainly by the movement of the antarctic surface water at the convergence where it sinks to form the intermediate layer.

The numbers in each line vary greatly, those in 0° being much higher than in the other two lines. In 90° E the 500–250 m. sample at Station 2811 was spilt during sorting aboard ship, and a large part of it was lost. It would evidently have been a key sample, and the contours from the other samples suggest that there would have been quite a large concentration there. I have indicated this by a dotted line in Fig. 5B.

S. marri is perhaps the most characteristic antarctic chaetognath of all, for although it lives in a water mass whose origins are found in the subtropics of the southern hemisphere, it only inhabits it when mixing and cooling have reduced it to the very precise conditions of temperature and salinity found in the warm deep water of the antarctic zone.

Eukrohnia sp. This species occurs very sparsely in the vertical sections, always below 1000 m. Its northern and southern limits are not yet known. It occurs in the antarctic zone as the commonest chaetognath below 1500 m.

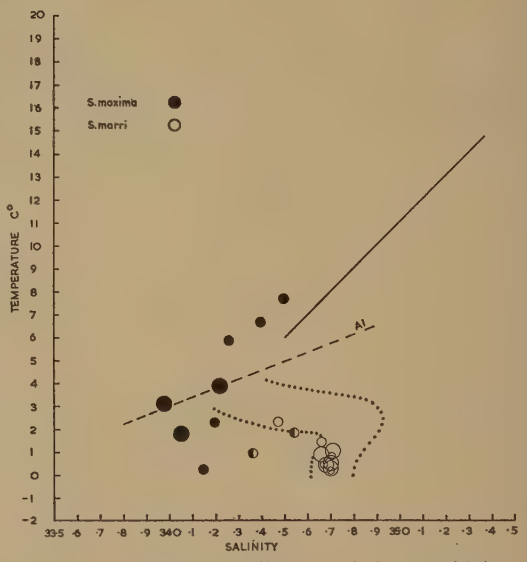


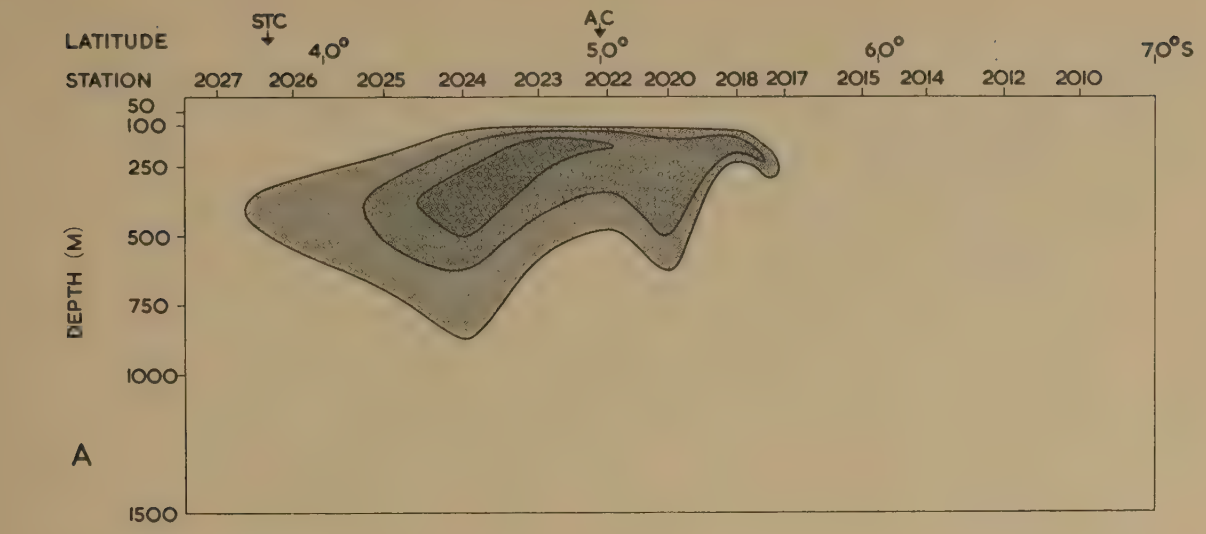
Fig. 6. The relative distribution of the two highest orders of abundance of *S. marri* and *S. maxima* in the 0° meridian in March, plotted against temperature and salinity. For explanation of the lines on the figure see legend to Fig. 4.

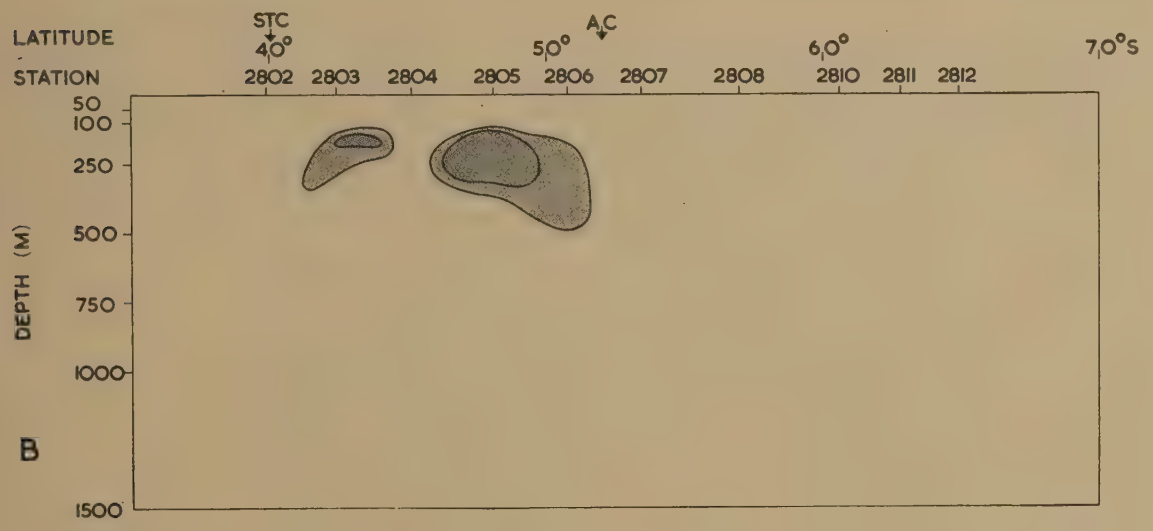
S. maxima (Fig. 7). This species is the subantarctic counterpart of *S. marri*. Its northern limit appears to be just within the subtropical zone at a depth of about 500 m., though it must extend considerably further north in some places as it has been found in both the Peru and Benguela currents. In the main, however, it is characteristically a subantarctic species. Its southern limit is usually not far south of the antarctic convergence, but it occurs in small numbers further south than this; in 80° W, for example, it occurs to the ice edge. These southerly records must be regarded as losses of population such as occur in *S. marri* to the north of its normal habitat, and in the case of *S. maxima* are probably due to mixing of the antarctic intermediate water with the warm deep water in the vicinity of the convergence.

The species is most numerous between 150 and 500 m. but extends in smaller numbers to 1500 m. It occurs very exceptionally in the subantarctic surface waters, but apparently never in the antarctic surface waters.

The main concentration of *S. maxima* is in the antarctic intermediate water, as reference to the temperature/salinity diagram (Fig. 6) shows, but it is also found on either side of this water mass. The salinity range for the larger concentrations is from 33·98 to 34·5 ‰ and the temperature range is from 0·3 to 7·3° C, a much wider tolerance than that of *S. marri*, reflecting perhaps the more varied conditions found in the moderate depths in the subantarctic zone.

The sections (Fig. 7) show that in 80° W the species extends in considerable numbers south of the antarctic convergence, while the other lines show the main concentrations ceasing well to the north





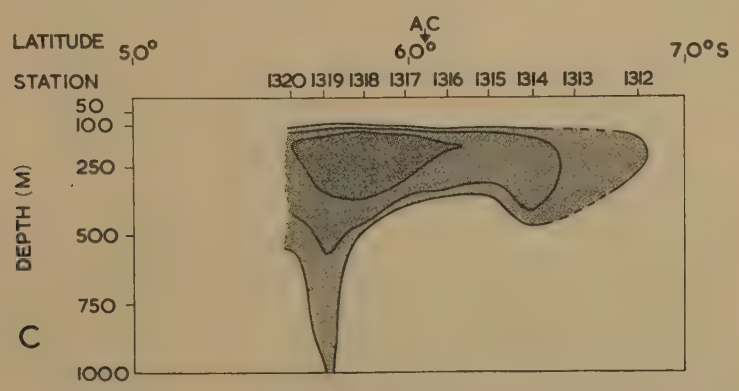


Fig. 7. The vertical distribution of *S. maxima* in 0° (A), 90° E (B) and 80° W (C). For numbers taken in each net see tables 4 *a–c* (p. 225).

of the convergence. The numbers vary considerably, those in 80° W being very much higher than those in 0°, while those in 90° E were very small indeed. It will be seen that the population in 90° E appears to be split into two parts, but it is doubtful if this is of any great significance as the numbers are relatively small, and if the species is patchy in distribution then the net at Station 2804, 250–100 m. may have missed the patch which would have linked the populations.

Table 3. *The occurrence of* S. macrocephala *in the lines of stations* 0°, 90° *E and* 80° *W*

Line	*Station*	*Depth*	*Number of specimens*
0°	2022	1500–1000	1
	2025	1000– 750	2
90° E	2802	1000– 750	1
		1500–1000	1
	2803	1000– 750	2
		1500–1000	1
	2804	1000—750	3
	2806	1500–1000	1
80° W	—	—	—

S. macrocephala. This species does not occur in numbers suitable for giving a contoured section, but in the lines under consideration it occurred at the stations shown in Table 3. It was not recorded from 80° W (possibly it was not recognized), but it has been taken by 'Discovery II' in the Western Pacific (Stations 2736, 2738, 2825, 2826) and from the South Atlantic sector (Stations 1771, 1772, 1773, 1775, 1776, 1777, 1805, 1807, 1808), so it seems likely that it also occurs in the Eastern Pacific. The species occurs in the tropics and subtropics and extends to the region of the West Wind Drift, though it is never present except in very small numbers in the Southern Ocean. It is rather more frequent in the Subantarctic than in the Antarctic.

The shallowest depth horizon at which it has been taken is 750–500 m., but this is exceptional. Johnston & Taylor recorded two specimens from a depth of 100 fms. (64° 34′ S 117° 1′ E), but this must be regarded as a mistake in identification as no other specimens have been taken at such a shallow depth. The species has been taken in nets down to 2400 m. but even in large (2 m.) nets at depths below 1000 m. the numbers caught have been very small, and one must conclude that it is an uncommon form in the Southern Ocean.

E. hamata (Fig. 8). It is not possible to define the northern limits of the distribution of this species, as it is one of the classic examples of bipolar distribution with tropical submergence. Its southern limit is the Antarctic continent. Its upper limit in the Southern Ocean is the surface, though immediately north of the subtropical convergence it is only found in deeper water. Its lower limit is below 1500 m. though it becomes less frequent in deeper water than it is in the top 500 m.

This species is by far the most abundant chaetognath in the Southern Ocean, and in all three sections it is very numerous. The section in 80° W, however, shows the greatest numbers with as many as 1275 specimens per 250 m. haul. The numbers in 0° are slightly less and those in 90° E least of all.

If this disparity in numbers is considered then it can be seen from fig. 8 that the pattern of distribution is essentially similar in all three lines. The maximum concentrations in each line are in the top 500 m, and the species is abundant to this depth in both the subantarctic and antarctic zones. The numbers decrease sharply at the subtropical convergence in 0°, and, although this decrease is not evident from fig. 8 *B*, in 90° E the actual numbers taken (see Table 4*b*, p. 227) fall off considerably at Station 2802 which was evidently just south of the convergence in that meridian. There is no fall off in numbers evident in 80° W but then the northernmost Station (1320) was probably 200 miles or more south of the convergence.

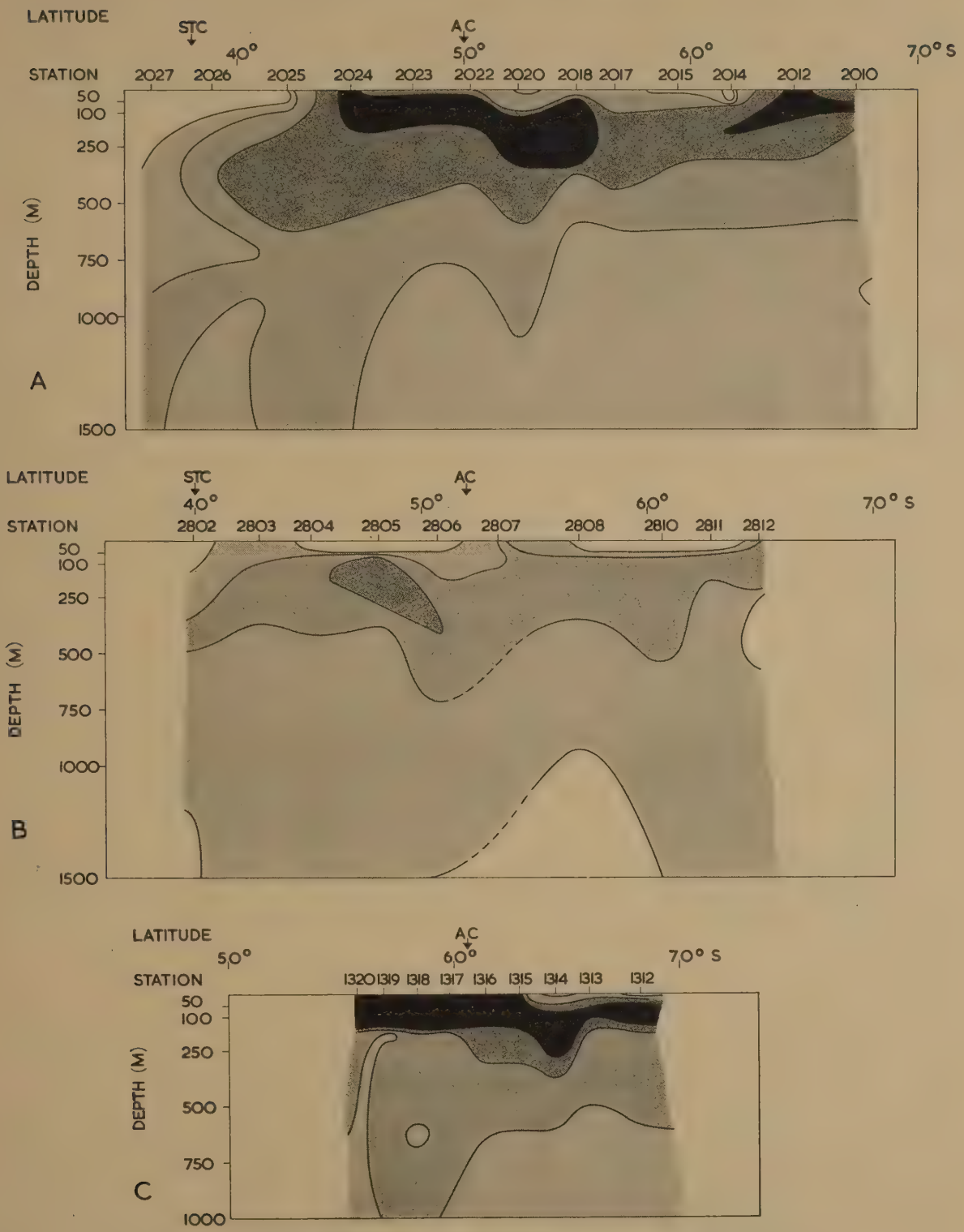


Fig. 8. The vertical distribution of *E. hamata* in 0° (A), 90° E (B) and 80° W (C). For the numbers taken in each net see tables 4 *a–c* (p. 225).

The temperature/salinity diagram (Fig. 9) shows that *E. hamata* can tolerate a wide range of temperature and salinity, as would be expected from such a cosmopolitan species. Nevertheless, I believe this wide degree of tolerance is more apparent than real, for in the Southern Ocean there are two forms or races of *E. hamata* analogous to the small northern and large southern races of *S. gazellae*, and I think that a careful study of the populations of *E. hamata* in the subtropics and tropics would show that there also the species consists of several ecologically separate races, all of which would be found to have much more precise physical and chemical requirements than would appear at present.

In unpublished informal reports Mr J. W. S. Marr, who made observations on this species for many years, has shown that mixing of the two Southern Ocean forms occurs seldom, but that where it does occur, as for example in the Falkland Island sector of the Antarctic, the mixing is indicative of similar mixing of the surface waters, and that the numbers of the 'foreign' race fall off sharply on each side of the convergence, showing that each race is intolerant of physical conditions on the 'other' side of the convergence. The variation, distribution and life history of *E. hamata* in the Southern Ocean might well form the substance for a separate report on its own and may one day be thus treated.

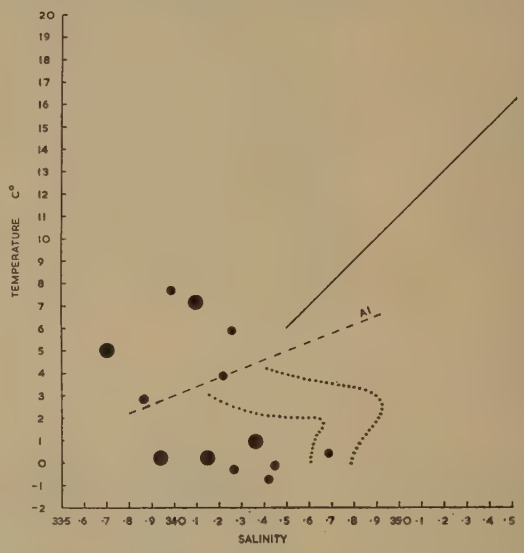


Fig. 9. The distribution of the two highest orders of abundance of *E. hamata* in the 0° meridian in March, plotted against temperature and salinity. For explanation of the significance of the lines on the figure see legend to Fig. 4.

S. serratodentata and *S. decipiens*. In the addition to the typical Southern Ocean species whose distribution is dealt with above there are two subtropical species, *S. decipiens* and *S. serratodentata* which occur in sufficient numbers south of the subtropical convergence to justify the sections shown in Figs. 10 and 11. *S. serratodentata* (Fig. 10) is often very numerous but almost completely restricted to the surface layers. *S. decipiens* (Fig. 11) is usually only present in smaller numbers and is restricted, at least in its main concentrations to the 500–250 m layer. Neither species extends more than 200 or 300 miles south of the Subtropical convergence.

H. mirabilis. This species does not figure on the vertical sections and there is little to add to Ritter-Zahony's description of its distribution. It is found below 2000 m., and in the Antarctic it probably inhabits the cold bottom water.

THE SEGREGATION OF SPECIES

In Fig. 12 the summer distribution of all the common southern chaetognath species is indicated. Inspection of Figs. 3, 5, 7, 8, 10 and 11 shows that the ranges of most of the species overlap extensively, but if only the maximum density of each species is considered, then it will be seen that there is no overlap. To show this point more clearly Fig. 12 has been constructed in which the contours of the two highest densities of each species of *Sagitta* have been superimposed upon one another in each section. In 0° and 90° E five species are shown, but in 80° W only three, since two species of subtropical origin are absent. It will be noticed that the main concentrations of the species do not overlap. Sometimes the second highest densities overlap, but not the highest. If *Eukrohnia hamata* (Fig. 8) is compared with these sections, it will be seen that it does overlap the highest concentrations of some of the other

species. It can also be seen from these sections that there are two populations of *S. gazellae*, representing the two races which occupy respectively the antarctic and subantarctic surface waters, while to the north *S. serratodentata* (see Fig. 10) occupies a similar habitat in the subtropical zone. In the deeper layers *S. marri*, *S. maxima* and *S. decipiens* (see Fig. 11) are distributionally analogous in the three zones.

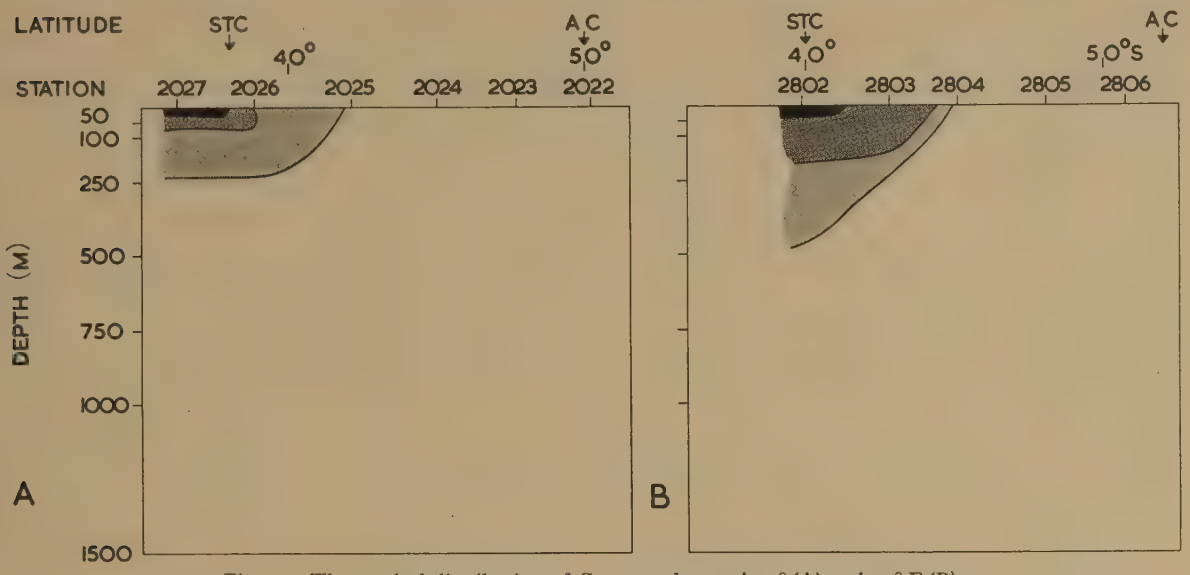


Fig. 10. The vertical distribution of *S. serratodentata* in 0° (A) and 90° E (B).

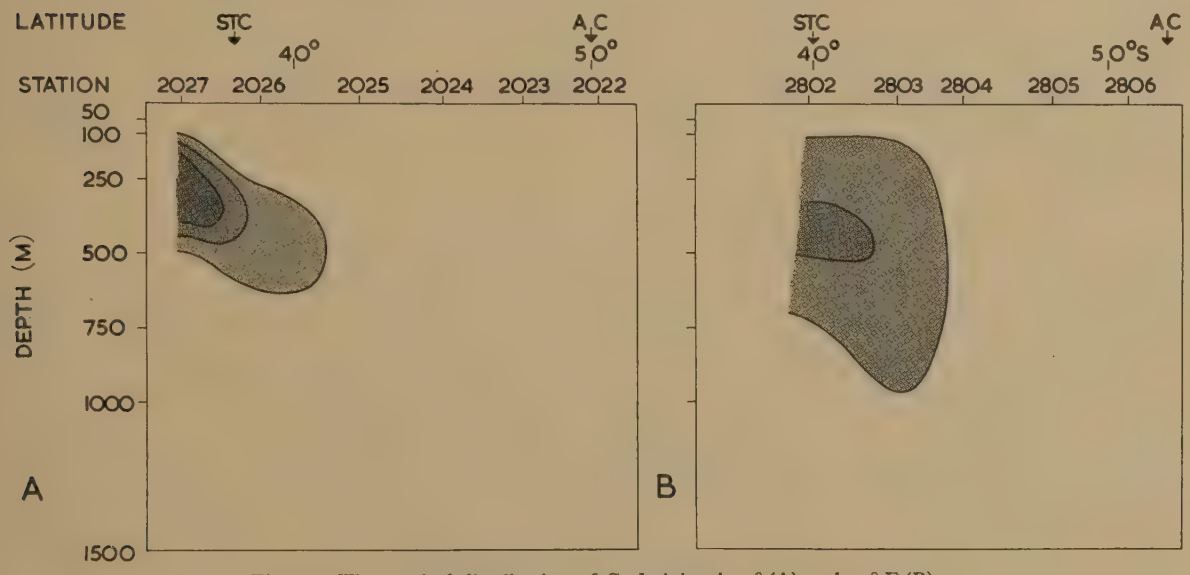


Fig. 11. The vertical distribution of *S. decipiens* in 0° (A) and 90° E (B).

This rather striking segregation of the species of *Sagitta* is of considerable interest, for although mixing does take place, there is no doubt that each species is concentrated in a particular area to the relative exclusion of the others, and it must be presumed that minor differences in the physical characteristics of these water masses are responsible for the segregation of the species, for reference to the temperature/salinity diagrams shows that most of the species can tolerate a greater range than that in which they are most abundant. This segregation must have been of considerable importance in

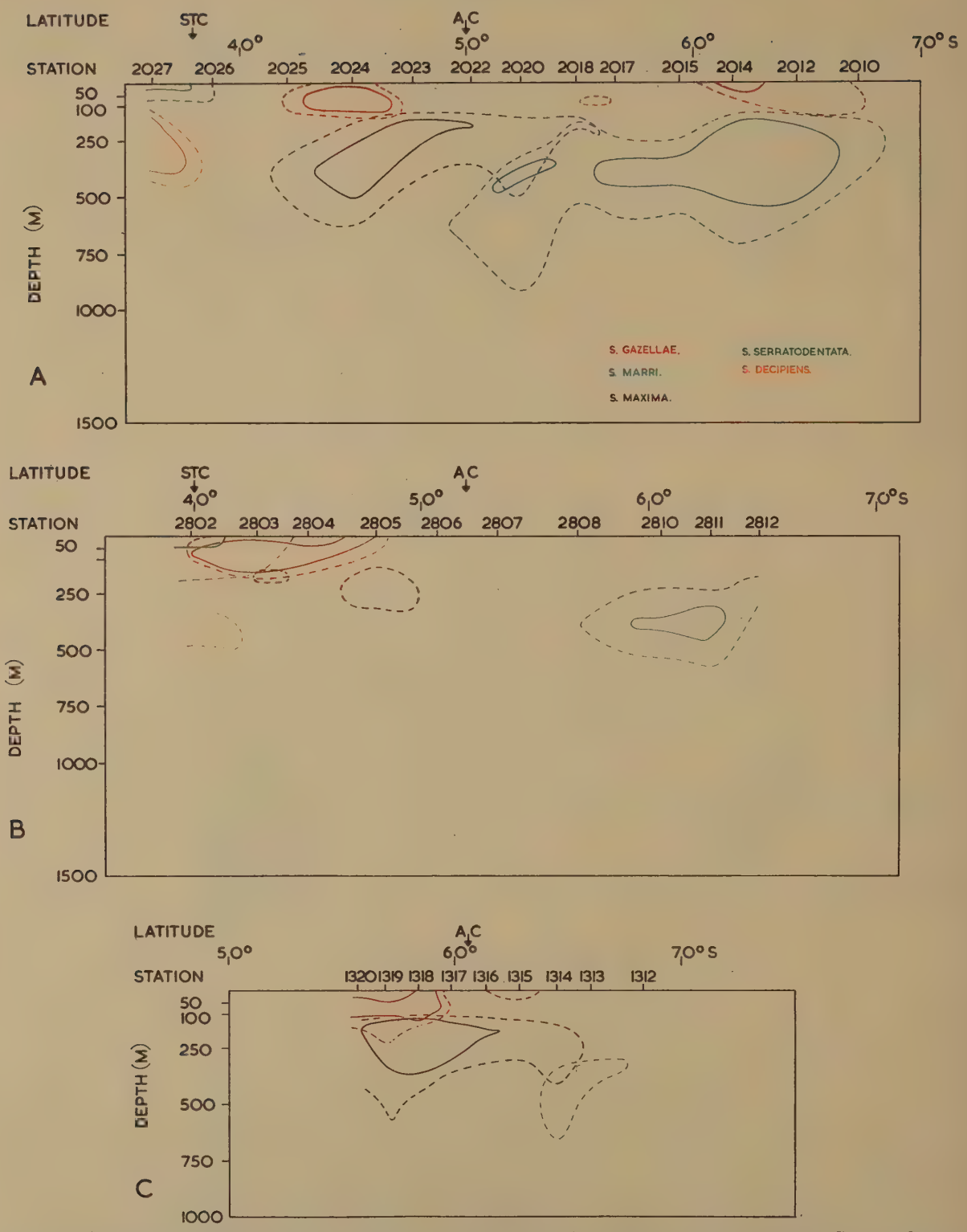


Fig. 12. The relative distribution of the two highest contours of density of *S. gazellae*, *S. marri*, *S. maxima*, *S. serratodentata* and *S. decipiens* in 0° (A), 90° E (B) and 80° W (C) (*S. serratodentata* and *S. decipiens* are not present in 80° W). The coloured contours should be compared with figs. 3, 5, 7, 8, 10 and 11.

originating and maintaining the species found in the Southern Ocean, and in this connexion it is not therefore surprising to find that when overlapping does take place it is between species of two separate genera, *Eukrohnia* and *Sagitta*, and not between species of the one genus.

WINTER DISTRIBUTION

Fig. 13 shows the vertical distribution of the four common species in 0° in August. At that time of the year the ice edge was in about 57° S, so that only a small part of the antarctic zone could be sampled.

S. gazellae. The main subantarctic concentration has moved from the surface layer down to the 250–100 m. horizon, but is still in the same latitudes. A small antarctic maximum appears in about 56° S which seems to be analogous with the March concentration (see Fig. 3) in the same latitude. This concentration also has descended from 100–50 m. to 250–100 m.

S. marri. The section does not go far enough south to sample the main part of the population of the species, and is therefore based on very small numbers which are not very informative. There is, however, a suggestion of a deeper winter distribution as found by Mackintosh (1937) for the 80° W line. An interesting feature of this section is the extension of part of the population into the Subantarctic in the 1500–1000 m. layer.

S. maxima. The main concentration is a little deeper in this line than it is in the summer one, and extends rather further south.

E. hamata. This species shows a clear movement to deeper water in the winter and possibly a slight southward extension of the main concentration.

Other species (not shown in the section). The August line in 0° does not commence so far north as the March one, so it is difficult to draw any conclusions about the subtropical species. *S. serratodentata* was present in very small numbers at Station 2385 at 250–100 m. and *S. decipiens* at the same station at 500–250 m. An August line (2867–2875) in the western Indian Ocean sector, which began just north of the subtropical convergence showed *S. serratodentata* present in the 50–0 m. haul in quite considerable numbers (465 per 250 m. haul) and *S. decipiens* present in the 500–250 m. horizon.

THE DISTRIBUTION OF THE MATURE STAGES

An interesting feature which is apparently common to all the most abundant Southern Ocean chaetognaths is the habit of descending into deep water to breed. This has been clearly shown for *S. gazellae* (David, 1955, p. 270). In *E. hamata* animals at states III and IV (Kramp, 1939) (see footnote, p. 204) are only found below 750 m., though animals at stage V ('var. *antarctica*') are sometimes found at the surface as well as in deep water. Specimens of *S. maxima* at stages III and IV are also found below 750 m. Very few specimens of *S. marri* at stage IV have been taken, but specimens at stage III are also only found below 750 m. These three latter species differ from *S. gazellae* in that the very young stages are found throughout the top 1000 m. of water, whereas very young *S. gazellae* are found only in the top 250 m.

It is difficult to imagine anything advantageous to the animals in this performance of deep spawning, which is also a habit of *S. lyra* and *S. planctonis* in the subtropics, but it is possibly a behavioural relic of some deep-living ancestral form. Since there are relatively fewer barriers to the spread of animals in deep water than there are to the spread of those at the surface, it seems quite likely that radiation in the group may have been via deep-living forms.

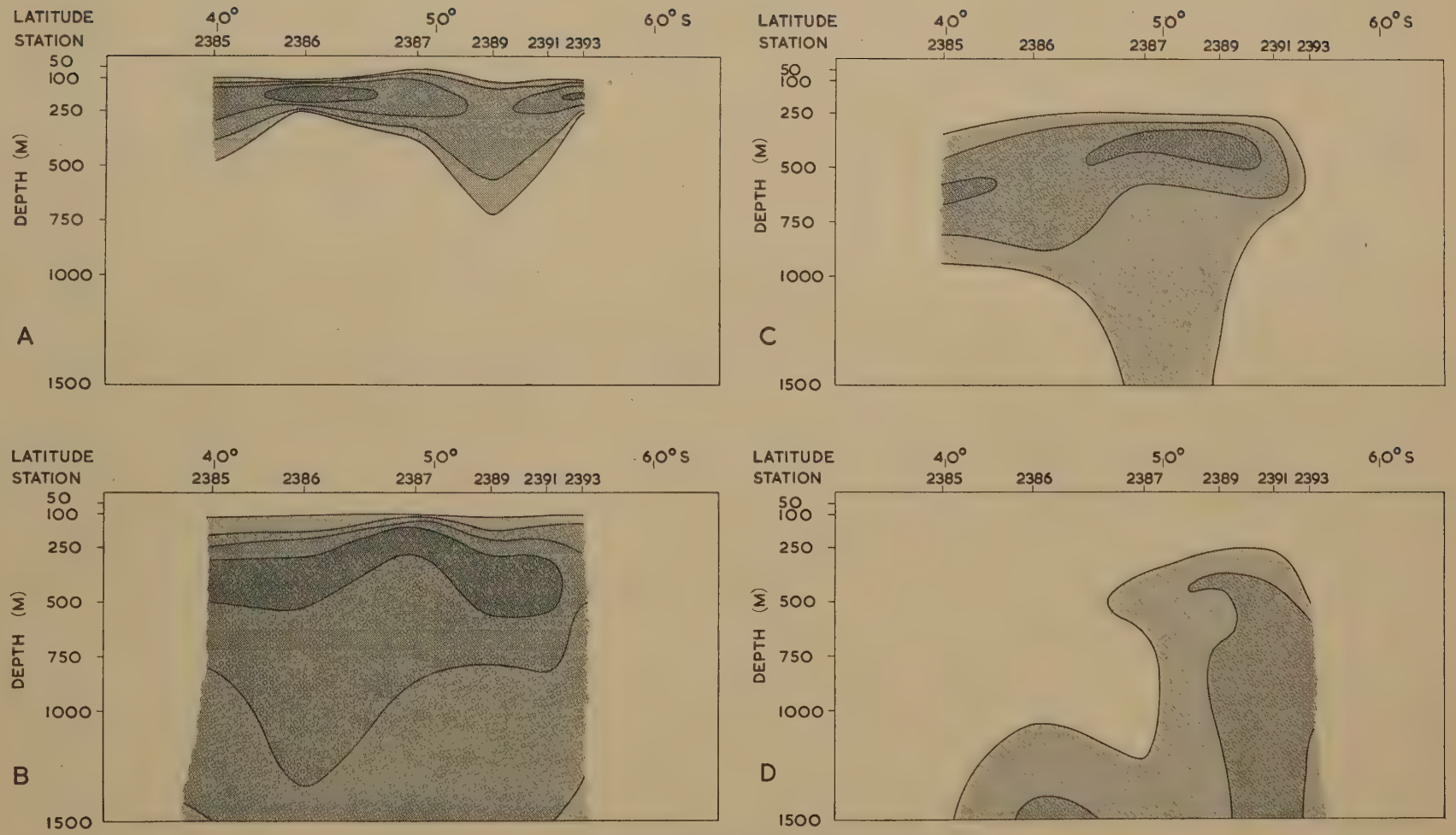


Fig. 13. The vertical distribution of (A) *S. gazellae,* (B) *E. hamata,* (C) *S. maxima* and (D) *S. marri* in the 0° meridian in August.

THE PATTERN OF DISTRIBUTION

The chaetognath fauna of the Southern Ocean is remarkable in the very small numbers of species present, seven only, living and maintaining themselves beneath a surface area of about 21 million square miles of sea, in comparison, for example, with the subtropical zone of the southern hemisphere which has not nearly so great a surface area yet contains at least sixteen species if not more.[1] This is, however, in keeping with the well-known principle that cold waters support fewer species than warm, though usually in larger numbers.

Among other points which emerge from this study is the fairly high proportion of endemic species —three out of seven. The antarctic benthic fauna is characterized by its high proportion of endemic species, which would be expected by virtue of its isolation, geographic and physical (covering temperature, salinity and other features), from the benthic fauna of the southern continents. The planktonic fauna would not be expected to be so subject to isolation, yet evidently from the data presented here it must be. The boundaries between water masses in the open ocean however are not usually clear cut and distinct, and large-scale swirls or eddies are probably produced where water masses meet. Salients of one water mass may from time to time be pinched off by another in the boundary region, and gradually absorbed. Thus the fauna carried in such a salient may be found outside its normal habitat; but such stray records should not be regarded as typical of the range of a species.

It is evident that barriers exist which limit the habitat of each species, and it seems likely that the convergence areas can be regarded as effective in this respect; nevertheless, there must also be other factors involved, and although temperature or salinity considered separately indicates that there is considerable overlap of tolerance in the various populations, the two factors in combination seem to have a considerable effect (see Figs. 4, 6 and 9). It is probable that if other physical factors were also considered in combination, the actual tolerance of each species would be circumscribed within precise and narrow boundaries; but it must be remembered that this would probably only mean that a particular species lived in a particular water mass, and that while the combination of physical factors identified the water mass, they might not necessarily be the factors governing the distribution of the species. Biological differences, as yet imperfectly understood, between various water masses, such as those which are being investigated by Wilson (1953, 1954) and Wilson & Armstrong (1954), may well play an important part in limiting the distribution of the plankton.

SUMMARY

The Chaetognatha of the antarctic and subantarctic zones can be classified broadly into three groups: (*a*) 'endemic' species, (*b*) species common to other regions, and (*c*) exotic species which do not maintain themselves in the area. There are three species in group (*a*), four in group (*b*) and eight in group (*c*). The horizontal distribution of these is discussed, and the vertical distribution of the seven species in groups (*a*) and (*b*) and two species of group (*c*) is shown by sections based on data from vertical closing nets worked in the Atlantic, Indian and Pacific Ocean sectors of the Southern Ocean. The results show that the distribution pattern is distinctive for each species, that the areas of maximum abundance of species of the genus *Sagitta* are mutually exclusive, and that despite the relative uniformity of the environment, these species are influenced by quite effective isolating factors.

[1] It is interesting to note that Tchindonova (1955, p. 307), commenting on the same phenomenon in the north Pacific, says: 'While there are 23 different species known for the Yellow Sea and the Sea of Japan out of which 16 are warm, and only two are cold water species, in the region of the Kurile-Kamchatka trench only seven species altogether have been found by us.'

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APPENDIX: TABLE 4

Table 4 (*a–c*)

Note: In this table the numbers of each species are corrected for a 250 m. haul (see p. 203). A horizontal dash indicates that a sample was missing and not examined, or that the weather prevented the haul from being made.

Table 4 *a*. *The March line in* 0°

Station no. ...	*2027*	*2026*	*2025*	*2024*	*2023*	*2022*	*2020*	*2018*	*2017*	*2015*	*2014*	*2012*	*2010*
S. gazellae													
50–0	0	0	5	30	5	15	0	0	0	0	55	30	10
100–50	0	10	25	90	10	5	0	20	20	10	15	35	35
250–100	0	3	12	8	10	7	10	12	7	3	3	3	5
500–250	0	1	2	1	1	5	3	1	0	1	0	1	0
750–500	0	0	0	0	0	0	2	2	0	0	0	0	0
1000–750	0	1	1	0	0	0	0	0	0	0	0	0	0
1500–1000	1	0	—	0	1	0	0	—	0	0	—	0	0
S. marri													
50–0	0	0	0	0	0	0	0	0	0	0	0	0	0
100–50	0	0	0	0	0	0	0	0	0	0	0	0	0
250–100	0	0	0	0	0	0	0	15	3	3	25	20	15
500–250	0	0	0	0	2	3	22	17	25	26	30	33	18
750–500	0	0	0	8	8	16	12	5	7	6	14	10	0
1000–750	0	0	1	10	1	2	11	0	7	2	3	1	1
1500–1000	0	0	—	1	0	4	7	—	1	1	—	2	0
S. maxima													
50–0	0	0	0	0	0	0	0	0	0	0	0	0	0
100–50	0	0	0	0	0	0	0	0	0	0	0	0	0
250–100	0	0	2	10	50	31	15	16	2	0	0	0	0
500–250	1	10	14	55	12	6	16	0	1	0	0	0	0
750–500	0	1	7	7	2	2	4	0	1	0	0	0	0
1000–750	0	0	0	4	2	0	2	2	0	1	1	0	1
1500–1000	0	1	—	0	3	1	2	—	0	0	—	0	0
E. hamata													
50–0	0	0	0	240	110	175	10	40	?	10	0	235	110
100–50	0	0	10	445	440	275	60	465	75	85	110	250	245
250–100	0	12	65	190	170	180	375	710	165	160	215	145	90
500–250	13	101	180	201	137	113	164	70	127	74	53	79	52
750–500	19	8	101	56	41	42	85	12	16	17	17	11	11
1000–750	18	29	37	38	10	11	28	13	8	5	8	10	20
1500–1000	36	6	—	16	17	12	15	—	7	5	—	0	3

Table 4*a* (*cont.*)

Station no. ...	*2027*	*2026*	*2025*	*2024*	*2023*	*2022*	*2020*	*2018*	*2017*	*2015*	*2014*	*2012*	*2010*
S. serratodentata													
50–0	620	20	0	0	0	0	0	0	0	0	0	0	0
100–50	15	20	0	0	0	0	0	0	0	0	0	0	0
250–100	5	8	0	0	0	0	0	0	0	0	0	0	0
500–250	0	0	0	0	0	0	0	0	0	0	0	0	0
750–500	0	0	0	0	0	0	0	0	0	0	0	0	0
1000–750	0	0	0	0	0	0	0	0	0	0	0	0	0
1500–1000	0	0	—	0	0	0	0	—	0	0	—	0	0
S. decipiens													
50–0	0	0	0	0	0	0	0	0	0	0	0	0	0
100–50	0	0	0	0	0	0	0	0	0	0	0	0	0
250–100	20	0	0	0	0	0	0	0	0	0	0	0	0
500–250	25	4	3	0	0	0	0	0	0	0	0	0	0
750–500	0	1	0	0	0	0	0	0	0	0	0	0	0
1000–750	0	0	0	0	0	0	0	0	0	0	0	0	0
1500–1000	0	0	—	0	0	0	0	—	0	0	—	0	0
S. lyra													
50–0	0	0	0	0	0	0	0	0	0	0	0	0	0
100–50	15	0	0	0	0	0	0	0	0	0	0	0	0
250–100	3	2	0	0	0	0	0	0	0	0	0	0	0
500–250	4	4	1	0	0	0	0	0	0	0	0	0	0
750–500	4	0	0	0	0	0	0	0	0	0	0	0	0
1000–750	3	2	0	0	0	0	0	0	0	0	0	0	0
1500–1000	12	0	—	0	0	0	0	—	0	0	—	0	0
S. macrocephala													
50–0	0	0	0	0	0	0	0	0	0	0	0	0	0
100–50	0	0	0	0	0	0	0	0	0	0	0	0	0
250–100	0	0	0	0	0	0	0	0	0	0	0	0	0
500–250	0	0	0	0	0	0	0	0	0	0	0	0	0
750–500	0	0	0	0	0	0	0	0	0	0	0	0	0
1000–750	0	0	2	0	0	0	0	0	0	0	0	0	0
1500–1000	0	0	—	0	0	1	0	—	0	0	—	0	0
S. zetesios													
50–0	0	0	0	0	0	0	0	0	0	0	0	0	0
100–50	0	0	0	0	0	0	0	0	0	0	0	0	0
250–100	0	0	0	0	0	0	0	0	0	0	0	0	0
500–250	0	0	0	0	0	0	0	0	0	0	0	0	0
750–500	1	0	0	0	0	0	0	0	0	0	0	0	0
1000–750	1	0	0	0	0	0	0	0	0	0	0	0	0
1500–1000	2	0	—	0	0	0	0	—	0	0	—	0	0

Table 4*b*. *The February line in* 90° *E*

Station no. ...	*2802*	*2803*	*2804*	*2805*	*2806*	*2807*	*2808*	*2810*	*2811*	*2812*
S. gazellae										
50–0	10	35	20	40	0	5	10	0	0	0
100–50	45	95	55	25	0	10	5	0	0	0
250–100	0	24	9	0	2	0	0	2	0	0
500–250	0	0	0	0	4	—	0	0	0?	0
750–500	0	0	0	0	1	—	0	1	0	0
1000–750	0	1	0	1	0	—	0	0	0	1
1500–1000	0	0	0	—	0	—	—	0	0	0

Table 4*b* (*cont.*)

Station no. ...	*2802*	*2803*	*2804*	*2805*	*2806*	*2807*	*2808*	*2810*	*2811*	*2812*
S. marri										
50–0	0	0	0	0	0	0	0	0	0	0
100–50	0	0	0	0	0	0	0	0	0	0
250–100	0	0	0	0	0	0	0	7	2	12
500–250	0	0	0	5	1	—	11	22	0?	8
750–500	0	0	0	2	0	—	1	2	5	0
1000–750	0	0	0	3	3	—	1	1	1	4
1500–1000	0	0	0	—	0	—	—	2	1	0
S. maxima										
50–0	0	0	0	0	0	0	0	0	0	0
100–50	0	0	0	0	0	0	0	0	0	0
250–100	0	10	2	27	5	0	0	2	0	0
500–250	3	1	3	3	7	—	0	0	2?	0
750–500	2	0	0	1	3	—	0	0	0	0
1000–750	2	2	0	1	2	—	0	0	0	0
1500–1000	0	1	0	—	0	—	—	0	0	0
E. hamata										
50–0	0	5	0	0	0	20	0	0	0	5
100–50	0	5	45	125	10	15	40	15	70	50
250–100	4	72	40	180	20	27	70	90	17	50
500–250	25	16	24	19	114	—	11	39	3?	0
250–500	13	24	3	13	21	—	2	10	9	3
1000–750	3	14	4	15	18	—	3	7	2	5
1500–1000	1	13	3	—	1	—	—	7	3	5
S. serratodentata										
50–0	715	65	0	0	0	0	0	0	0	0
100–50	115	10	0	0	0	0	0	0	0	0
250–100	24	0	0	0	0	0	0	0	0	0
500–250	4	0	0	0	0	—	0	0	0?	0
750–500	0	0	0	0	0	—	0	0	0	0
1000–750	0	0	0	0	0	—	0	0	0	0
1500–1000	0	0	0	—	0	—	—	0	0	0
S. decipiens										
50–0	0	0	0	0	0	0	0	0	0	0
100–50	0	0	0	0	0	0	0	0	0	0
250–100	2	3	0	0	0	0	0	0	0	0
500–250	13	4	0	0	0	—	0	0	0?	0
750–500	8	1	0	0	0	—	0	0	0	0
1000–750	0	3	0	0	0	—	0	0	0	0
1500–1000	0	0	0	—	0	—	—	0	0	0
S. lyra										
50–0	0	0	0	0	0	0	0	0	0	0
100–50	0	0	0	0	0	0	0	0	0	0
250–100	15	0	0	0	0	0	0	0	0	0
500–250	7	0	0	0	0	—	0	0	0	0
750–500	0	1	0	0	0	—	0	0	0?	0
1000–750	2	1	0	0	0	—	0	0	0	0
1500–1000	0	0	0	—	0	—	—	0	0	0
S. macrocephala										
50–0	0	0	0	0	0	0	0	0	0	0
100–50	0	0	0	0	0	0	0	0	0	0
250–100	0	0	0	0	0	0	0	0	0	0
500–250	0	0	0	0	0	—	0	0	0?	0
750–500	0	0	0	0	0	—	0	0	0	0
1000–750	1	2	3	0	0	—	0	0	0	0
1500–1000	1	1	0	—	1	—	—	0	0	0

Table 4 *c*. *The August line in* 0°

Station no. ...	*2385*	*2386*	*2387*	*2389*	*2391*	*2393*
S. gazellae						
50–0	0	0	0	0	0	0
100–50	0	0	5	0	0	0
250–100	17	40	17	9	12	19
500–250	5	0	1	7	6	1
750–500	0	0	0	3	0	0
1000–750	0	0	1	0	0	0
1500–1000	0	3	0	0	0	0
S. marri						
50–0	0	0	0	0	0	0
100–50	0	0	0	0	0	0
250–100	0	0	0	0	0	0
500–250	0	1	1	5	4	0
750–500	0	0	1	4	8	7
1000–750	0	0	0	7	9	7
1500–1000	0	6	2	4	9	2
S. maxima						
50–0	0	0	0	0	0	0
100–50	0	0	0	0	0	0
250–100	0	0	0	0	0	0
500–250	1	7	12	14	6	1
750–500	12	7	3	5	6	0
1000–750	3	6	1	1	0	1
1500–1000	0	0	2	2	1	0
E. hamata						
50–0	0	0	0	0	0	0
100–50	0	0	0	0	0	0
250–100	4	10	160	8	25	27
500–250	134	196	82	207	197	73
750–500	106	73	78	87	89	28
1000–750	26	110	48	31	40	16
1500–1000	15	29	22	10	18	14
S. serratodentata						
50–0	0	0	0	0	0	0
100–50	0	0	0	0	0	0
250–100	10	0	0	0	0	0
500–250	0	0	0	0	0	0
750–500	0	0	0	0	0	0
1000–750	0	0	0	0	0	0
1500–1000	0	0	0	0	0	0
S. decipiens						
50–0	0	0	0	0	0	0
100–50	0	0	0	0	0	0
250–100	0	0	0	0	0	0
500–250	7	2	0	0	0	0
750–500	0	0	0	0	0	0
1000–750	3	0	0	0	0	0
1500–1000	2	0	0	0	0	0
S. macrocephala						
50–0	0	0	0	0	0	0
100–50	0	0	0	0	0	0
250–100	0	0	0	0	0	0
500–250	0	0	0	0	0	0
750–500	0	0	0	0	0	0
1000–750	0	1	1	0	0	0
1500–1000	0	2	0	0	0	0

PLATE X

An antarctic and an arctic specimen of *S. maxima* at the same stage of maturity. $\times 2\frac{1}{4}$ approx.